Melding ecology, classical weed biocontrol, and plant microbial ecology can inform improved practices in controlling invasive plant species

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Abstract

Early research leading to the successful biological control of invasive species such as *Opuntia* spp., and *Hypericum perforatum* set examples and provided data useful for research programs that would follow. However, this early work failed to become established as a source of applicable principles for later workers in weed biocontrol. Recently, retrospective and parallel studies have been suggested as a means to reengage with earlier work to derive useful ideas and data to enhance future programs in weed biocontrol. Parallel studies by workers in plant community ecology on the nature of feedback elicited by plant species in their invaded and native range have shown the importance of soil microbial communities in effecting feedback. Retrospective reexamination of previous studies would likely provide clues to other insect–plant pathogen interactions in addition to those described by the author and others. The effects of invasive species in profoundly altering soil microbial communities point to the need for further studies on key microbial species contributing to or driving the impact of biocontrol. These collective data suggest that the desired goal of selecting for and utilizing stronger biocontrol agents to reduce nontarget effects and to increase the impact of biological control programs would be best served by prerelease studies that assess the propensity of a candidate agent for direct or indirect interaction with other agents. This could be assessed through the use of survival analysis. Overall, parallel empirical and retrospective studies should be a necessary part of how biological control is practiced.
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1. Introduction

The recognition of the potential of insect–plant pathogen interactions came early in the history of biological control of weeds. In the two founding projects in weed biocontrol, early workers documented the role of microbes in the successful impact on the target weed or their potential to contribute to impact. For example, the contributions of fungi and soft-rotting bacteria to the destruction of *Opuntia* spp. (Cactaceae) in conjunction with larvae of *Cactoblastis cactorum* (Bergroth) (Lepidoptera: Pyralidae) were noted (Dodd, 1940). In summing up the lessons to be derived from the long-term project that resulted in the successful control of *Hypericum perforatum* L. (Hypericaceae), it was recommended that insects should be sought that could cause "encouragement" of plant pathogens (Wilson, 1943). Despite such findings, there followed a long lag period until the topic was revived in a concrete way by beginning in 1978 with studies that reported on the nature of an apparent insect–plant pathogen interaction in the biological

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control of water hyacinth (Charudattan, 1986; Charudattan et al., 1978). Subsequent to this revival, other workers assessed data from weed biocontrol research conducted in the intervening years and made findings that can easily be related to the theme of insect–plant pathogen interactions as a key to classical weed biocontrol. For example, it was noted that in 70–80 cases of successful biological control, one or two insects were responsible (Denoth et al., 2002; Myers, 1985). This evidence should have prompted investigations into the mechanisms by which these successful insects impacted the plant, thereby initiating the development of a body of theory useful in subsequent biocontrol programs. However, at no time was such an approach suggested. The findings also call into question whether it is a viable approach to seek to construct successful "guilds" of insect agents to control invasive weeds. Similar to the regret that Myers expressed with regard to the paucity of quantitative data on impact by agents (Myers and Bazely, 2003), failure to develop data on modes of action by successful agents has also been unfortunate. Investigation of mechanisms of agent impact would likely have yielded clues that could then be investigated and tested in devising criteria tailored to select agents against invasive species. However, a consistent practice to search for and release as many host-specific insects as possible was bound to quickly surpass a point of diminishing returns. In subsequent biocontrol programs, control of herbaceous perennial weeds might have been achieved sooner, more consistently, and with fewer resources had prior research knowledge been used to develop an applicable body of theory.

Reexamination of what little data there is on the reasons underlying success of a given insect against an invasive weed could still provide information useful for advancing and refining future projects. For example, the success of *Chrysolina* spp. (Coleoptera: Chrysomelidae) in controlling *H. perforatum* in California, presumed to be caused by increased susceptibility to drought as a result of the effects of herbivory by this agent (Holloway and Huffaker, 1951), might have been overlooked as an insect–pathogen interaction. One could reach this conclusion because of the seldom-mentioned detail that larvae of *Chrysolina* attack and destroy the winter procumbent growth of *H. perforatum* (Holloway, 1964). Thus, most of the damage was done prior to the onset of the dry summer in California and before the leaf-feeding adult beetles emerged. The prolonged period of attack by larvae of *C. hypericum* on the basal growth of the plant could be the stage at which the insect creates avenues for ingress by plant pathogenic or deleterious microbes. Retrospective analysis of this possibility could yield valuable data for developing concepts useful in achieving greater impact in future programs with similar weed targets. For example, it might be revealing to reexamine this agent/target weed system for local

associations similar to that of the fungus *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. in Penz. (anamorphic Phyllachoraceae) with damage to this weed by *Chrysolina hyperici* (Forst.) found to occur in Ontario, Canada (Hildebrand and Jensen, 1991). Similarly, retrospective analysis of the mechanism (or etiology) of control of *Lythrum salicaria* L. (Lythreceae) could be useful because both the root-boring beetle *Hylobius transversovittatus* Goeze (Coleoptera: Curculionidae) and the leaf beetle *Galerucella calmariensis* L. (Coleoptera: Chrysomelidae) cause root damage which could allow infection by soilborne plant pathogens.

There is at least one example of actual retrospective analysis that has essentially confirmed previous findings in the scientific literature about the mechanism of control of a target weed. A partial reassessment of the *Opuntia–Cactoblastis*–microbial system has confirmed that several fungi may play a role in the destruction of cladodes of the cactus (Martin and Dale, 2001) as originally described (Dodd, 1940).

1.1. Negative feedback and invasive species: where ecology, weed biocontrol, plant pathology, and horticulture converge

Recent findings have shown that invasiveness versus rarity of plant species is related to differential responses to their own soils and that negative feedback develops slower for more common, invasive species than for rare species (Klironomos, 2002). Rare species exhibit an intensely negative differential growth response to their soil versus soil from other species, whereas invasive species respond positively, with better growth in soils of other plants. Sterilization can often be shown to decrease the effect, indicating the role of the soil microbial community. It would be mistaken to conclude that nonnative soils or soils where exotic plant invasion is occurring necessarily provide positive feedback. Further, any inference that it is inherent that invasive species necessarily elicit positive feedback fails to account for the dynamics of soil microbial communities in response to individual plant species (Ehrenfeld et al., 2001; Kourtev et al., 2002, 2003). A series of studies compared the differential effects on soil properties and functions of an invasive C_4 grass, *Microstegium vimineum* (Trin.) A. Camus., an invasive woody shrub, *Berberis thunbergii* DC (Berberidaceae), and a native woody shrub, *Prunus serotina* Ehrh. (Rosaceae). These studies showed that both exotics changed soil functions and properties (e.g., pH and nitrification rates) (Ehrenfeld et al., 2001), and both microbial community function and structure (enzyme activities and substrate-induced respiration were correlated with microbial community structure, as characterized using phospholipid fatty acid profiles) (Kourtev et al., 2002). These changes were suggested as being fundamentally long-term (Kourtev et al., 2003) and capable

of hindering restoration of native communities (Ehrenfeld, 2003).

That soil-based feedback could accelerate invasion and render restoration of native communities, more difficult could be based on changes that included higher levels of individual pathogens or deleterious microbes that could effectively prevent attempts to re-establish native plants. This would depend on whether the inoculum potential of these deleterious organisms, causing pre- or postemergence damping-off of seedlings, are favored by such a feedback.

Rare species may develop a negative feedback sooner, whereas more common and invasive species likely cause a more gradual response (Klironomos, 2002). An in-depth background on negative feedback comes from the research on a horticultural problem that becomes apparent when tree fruits are replanted in the same orchard or vineyard soils following removal of the previous planting. Termed "replant" (Sewell, 1984) or "sick soil" syndrome (Vancura et al., 1983), it describes the poor growth response most prominently of tree fruit species to soil microbial communities that develop in soils in which they are grown. Rosaceous fruit species often experience severely reduced growth when successive vineyards or orchards are planted on the same site. It is also experienced in nursery settings with the continuous replanting of young trees for propagation prior to their use in establishing or re-establishing orchards. The nursery replant syndrome can be partially alleviated by treating planting stock with bacteria antagonistic to plant pathogenic fungi such as *Pythium*, *Fusarium*, and *Rhizoctonia* spp. (Caesar and Burr, 1987). Apparently, the fungal component of the replant syndrome is more affected by the bacteria applied than the prokaryotic component.

Most invasive plants of concern to land managers in the rangelands and prairies of North American are herbaceous perennials or long-lived biennials. There have been only a few studies on the effects of herbaceous perennials in altering soil biotic and physical properties. However, studies based on a model of the rosaceous species *P. serotina*, the invasive shrub *B. thunbergii*, and the C_4 grass *M. vimineum* (discussed above) provide an interesting intersection between plant ecology, invasiveness, and plant microbial ecology. These studies on the effects of feedback and microbial communities on growth of invasive woody perennials (Packer and Clay, 2003; Reinhart et al., 2003), and vice versa provide highly pertinent themes for similar studies with exotic, invasive herbaceous perennials but these types of studies remain lacking. For example, in addition to the findings described above for the invasive *B. thunbergii* and C_4 grass species, studies on the effects of *P. serotina* in its native and invaded ranges detailed the spatial and temporal aspects of negative feedback associated with this woody species. Biomass of conspecific seedlings and sap-

lings was found to be correlated with distance from mature *P. serotina* trees (Packer and Clay, 2003). It was also concluded that the invasion of this species in Europe is facilitated by the soil community (Reinhart et al., 2003) and that feedback can develop rapidly at the spatial scale of a single seedling (Packer and Clay, 2004). These authors and their coworkers have further concluded that microbial community-partitioned nutrient pools essentially generate the nature of the feedback that will drive plant community succession and diversification (Reynolds et al., 2003). Whether these latter findings are more applicable to a deeper understanding of the horticultural replant problem or may suggest avenues for future studies on invasive herbaceous perennials should be pursued. Nonetheless, these studies apparently mean that both biocontrol and restoration will be affected significantly by negative feedback.

Recent studies concerned with the effect of microbial feedback on plant population dynamics (Bever et al., 1997), the effects of such feedbacks on plant communities (Klironomos, 2002; Van der Putten et al., 1993), and the nature of feedback in relation to invasive plants (Callaway et al., 2004; Klironomos, 2002) point clearly to the importance of soil microbes on the ecology of exotic invasive plants. These research themes corroborate studies by the author and others (Brinkman et al., 1999; Caesar, 1994a,b, 1995, 1996, 2000; Caesar et al., 1993, 1996a,b, 1999, 2002; Kremer et al., 2005) that are contemporaneous with the feedback work, showing the importance of soilborne plant pathogens and deleterious rhizosphere bacteria on exotic invasive species. At the same time, despite mention in some major texts on biological control, recognition of the possible strong effects of microbes, whether as single species or communities of species in combination with insects, has been generally lacking. Understanding how microbial communities affect invasiveness and in turn how they are affected by invasive plants is a key to adapting and revising current methods for biological weed control to be more productive and safer.

A series of recent studies concluded that invasive plants experience a positive feedback in their nonnative soils, while in general, they are impacted negatively by their indigenous soil biota (Callaway et al., 2004; Klironomos, 2002; Packer and Clay, 2004; Reinhart and Callaway, 2004). The effect has been indicated to be one of the cultivating soil biota with increasingly positive effects by the nonnative species (Callaway et al., 2004), and by extension, an invading species. We should consider whether this is actually a lack of negative feedback accompanied by a transient stimulation of nutrient availability and/or increased bacterial activity along with reduced fungal activity resulting from soil fumigation or mechanical disturbance of the soil (a general principle in agronomic science) in the conduct of the studies. The overall effects, however, are the important

contrasting effects of native versus nonnative soil biota on an invading plant species. The author would suggest that in the case of an apparent positive feedback seen in the invaded range, one is actually observing the absence of negative feedback as the initial phase of the plant/soil biota dynamic ultimately leading to the establishment of negative feedback. The as-yet rare stand declines of *Euphorbia esula/virgata* L. (Euphorbiaceae) documented by the author in the Northern Plains of the USA (Caesar, 1996) and the existence of a complex of microbes (Caesar, 1994b, 1996; Caesar et al., 1993, 1996a) associated with such declines could indicate the onset of negative feedback. That negative feedback is more pervasive in Eurasia, the native range of *E. esula/virgata* would be expected given the occurrence of this species in those soils over geologic time.

Insect–pathogen interactions would have the long-term effect of accelerating, increasing, and maintaining the negative feedback by a constant turnover of inoculum to the soil caused by cycles of insect damage with increased root infection, death of the root, and deposition of propagules to soil (Caesar, 2003). The effectiveness of biological control releases of root-attacking insects may have as a prerequisite the advent of a threshold of negative feedback or buildup of plant pathogens for insect–plant pathogen synergism to be effective.

For at least two invasive perennial species of concern in North America, *E. esula/virgata* and *Centaurea maculosa* Lam., an insect–plant pathogen association is found throughout the native Eurasian range of these species. Stands of these species in their native range are typically sparse and unthrifty (Caesar et al., 1998, 2002). When colonized by root-attacking insects, plants are typically infected with a complex of plant pathogenic fungi (Caesar et al., 1996b, 1998, 2002). These findings and those discussed above provide evidence that insect–plant pathogen interactions facilitate and often accelerate negative feedback. This scenario is supported by data developed by the author, indicating that there are higher levels of *Fusarium* spp. in the rhizosphere soils of stands of *Euphorbia* under continued attack by larvae of an insect (Caesar, 2003). Others also have shown that root attack by invertebrates hastens the development of negative feedback (e.g., Van der Stoel et al., 2002).

1.2. Ecological literature and the retrospective analysis of the biocontrol literature: the basis for more successful weed biocontrol in the future

If retrospective studies can aid ongoing and future programs, as proposed recently (Caesar, 2000; Louda et al., 2003; Myers, 2000; Myers and Bazely, 2003), especially to support greater ecological safety, then failure to account for insect–plant pathogen interactions could undermine such efforts. If the goal is to select successful biocontrol agents by looking at agents successful in the past, then it is imperative to focus on agents capable of synergism. The increasingly recognized necessity to attain a greater level of impact (Pearson and Callaway, 2003, 2004, 2005) by agents to reduce nontarget effects can be achieved through a more precise and rational process of agent selection (Caesar, 2004). This aim requires the application of recent findings of the importance of plant pathogens to the mortality of perennial weeds (Caesar, 2003) as well as retrospective assessment of data from older studies (Dodd, 1940; Wilson, 1943) which essentially indicate that capacity for synergism be a paramount criterion for agent selection.

Workers who have recommended schemes or criteria (summarized in Myers and Bazely, 2003) have not accounted for the patterns and recommendations made by the two original studies that were successful (Dodd, 1940; Wilson, 1943). Such an omission is due to the compartmentalization of weed biocontrol research and the general lack of an interdisciplinary approach to weed biocontrol research (Caesar, 2000). Narrowly based programs, consisting of research teams predominantly or wholly of a single scientific discipline, are less likely to be capable of dealing with barriers that cannot be solved with traditional approaches. This may be the greatest barrier to success of biocontrol programs in the future. For example, a weed biocontrol program no longer has the unrestricted option to engage in searches for additional insects leading to further releases as a strategy in response to the failure of an initial set of releases of the agent to impact the weed. Multiple releases of ineffective agents have ultimately increased the real and perceived threat to nontarget species. Empirical approaches to assessing agents have rarely been put forth with the occasional notable exception such as the recommendation that life-table analysis be applied to assess the impact of agents on weeds (McEvoy et al., 1990) or a quantitative study on the impact of a rust disease of two invasive *Centaurea* spp. (Shishkoff and Bruckart, 1996). Such key factor, k value-based analysis, as in the former instance, has not been widely used in plant-related studies of factors causing mortality. For example, k value analysis would be most useful if applied to changes in plant density due to mortality in response to herbivory. In respect to insect herbivory, the life-table analysis assumes that insects themselves cause mortality. This assumption may not strictly hold given the large body of evidence that direct interactions with plant pathogens can cause mortality of the host (Caesar, 2003; Dodd, 1940; Paine et al., 1997; Stipes and Campana, 1981).

Myers and Bazely (2003) point out that Charles Darwin was one of the first to assert that an escape from herbivores was related to the capacity of a plant species to be invasive (Darwin, 1859). Despite several attempts at reassessment of what has been called the enemy-release hypothesis, this hypothesis has never been effectively

refuted (Keane and Crawley, 2002; Mitchell and Power, 2003; Torchin et al., 2003), and the enemy-release hypothesis has come to constitute an underlying basis for biological control of weeds. Attempts to resolve the relative importance of escape from enemies versus the biotic-resistance hypotheses are hindered by a failure to consider the role that microbes can play in conjunction with insect damage in causing mortality. Thus, a sole focus on any singular biotic factor for any ecological process would likely lead to erroneous assumptions. However, that "keystone" species exist in these invasive species/natural enemy systems should not be overlooked. Species such as overt soilborne plant pathogens (*Rhizoctonia* spp.), which exist below the limit of detection in soil by conventional methods, are consistently found in the insect-wounded tissues of invasive weeds such as *E. esula/virgata* and *C. maculosa* (Caesar et al., 1996a, 1998, 2002). The soilborne plant pathogen *Rhizoctonia solani* Kühn (Anamorphic Corticiaceae) has been shown to be >2.5 times more likely than *Aphthona* spp. flea beetles alone to cause mortality of *E. esula/virgata* (Caesar, 2003). A complex of plant pathogens was found in the tissues of dead and dying plants where effective biocontrol of *E. esula/virgata* L. or *C. maculosa* was occurring (Caesar, 1995; Caesar et al., 1996a). A similar complex of soilborne plant pathogens occurs on these species in Eurasia (Caesar, 1995; Caesar et al., 1996a, 2002). The higher contribution of plant pathogens versus insects to mortality of leafy spurge shown experimentally using microcosms supports a connection between insect damage and infection by soilborne plant pathogens in the rapid mortality of the target weed (Caesar, 2003). This finding reinforced the correlation between the successfully impacted sites and the presence of soilborne plant pathogens within dead and dying, insect-wounded plants (Caesar, 1995). Plant pathogens, in conjunction with insect herbivory, can have profound effects on plant populations and communities. The Dutch Elm disease is but one example. That plant community dynamics are generally driven by multitrophic interactions are now well established in the ecological literature (Van der Putten and Van der Stoel, 1998; Van der Stoel et al., 2002). However, acceptance of this idea in the area of weed biocontrol has been slow.

Assessment of candidate agents for their capability for direct interactions should have priority because of the ecological significance of their synergisms. Insect–plant pathogen synergistic interactions have had widespread, rapid, and highly destructive impacts. There is a consensus among researchers in the area of weed biocontrol that prerelease studies focused on the likelihood of strong impact are imperative for a variety of reasons including reduced nontarget risks and other unintended negative effects (Balciunas, 2004). The aim of attaining high impacts are best served by assessing the ability of a given agent to synergize with at least one other agent

(Caesar, 2003). Additionally, any proposed approaches to weed management that emphasize restoration of plant communities or revegetation with competitive species will be handicapped by a lack of accounting for such microbial effects as negative feedback and soil functional changes on plant community dynamics.

2. Conclusions

Screening of potential agents should include prerelease studies to examine the effects of combinations of insects and plant pathogens or deleterious microbes. Such an approach supports a goal of increasing impacts and reducing direct and indirect nontarget effects. Findings and conclusions by others independently support the importance of employing strong biocontrol agents as well as the importance of belowground multitrophic interactions on succession in natural vegetation (Pearson and Callaway, 2004, 2005; Van der Putten, 2003).

The existence of genuine positive feedback (as compared to actually being an absence of negative feedback, as discussed earlier) should be investigated further. In addition to the studies cited herein which infer the existence of positive feedback, there are indications that such a phenomenon may exist in the case of bacterial functional groups (e.g., antibiotic-producing *Bacillus* or *Pseudomonas* spp.) that vary according to the management regime (Garbeva et al., 2003, 2004). Full confirmation would require studies of the effects of individual and combinations of predominant microbial species on the plant species in question.

Programs for classical biological control of exotic, invasive weeds can benefit from a variety of interdisciplinary approaches, informed by philosophies and doctrines taught within individual fields and their interplay. Thus, integration of both insect-based and plant pathogen-based approaches to weed biological control may markedly increase the strength of the impact of the agents released and thereby lead to more rapid success of programs.

No approach to modeling or predicting invasiveness or investigation of underlying theory, as part of developing new approaches for success or restoration, can be fully successful if it fails to account for soil biota. Well-founded, empirical studies have made this conclusion virtually inescapable.

Retrospective and parallel studies can be valuable in improving protocols for selecting agents against present and future target weeds. Retrospective studies can include experiments as well as observations of successful biocontrol systems to elucidate the mechanisms of control. For example, the extent of involvement of root-infecting plant pathogens in the control *H. perforatum* and *L. salicaria* should be investigated.

The state of feedback development, which the author infers to be occurring in the case of *E. esula/virgata* and possibly *Centaurea* spp., may affect whether and when insects released to control a perennial weed will be successful. Against the background of an incipient establishment of negative feedback against *E. esula/virgata*, the release and establishment of the biological control agent *Aphthona* spp. could be both benefiting from accrued negative feedback and further accelerating it. As a "flow-on" effect of this dynamic, it could be expected that higher soil population levels of soilborne plant pathogens would result (Caesar, 2003). This is an effect noted also in the case of *Tamarix* species (Rekah, 2001).

The multiple standards of "success" of a weed biocontrol program set forth recently (Anderson et al., 2000, also summarized in Myers and Bazely, 2003) are probably not valid. There should be a single standard of success: significant reduction in density of the targeted weed, defined as "biological success" (Anderson et al., 2000). Only when such success is achieved would it then be valid to specify elements of that success, such as political success or economic success. Such subelements of success cannot validly and credibly serve in place of actual success based on stand reduction. This is the explicit or implicit goal of every invasive weed control program.

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